Weed Science 2008 56:834–840

Maternal and Burial Environment Effects on Seed Mortality of Velvetleaf (*Abutilon theophrasti*) and Giant Foxtail (*Setaria faberi*)

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The primary defense against seed mortality, the seed coat, is maternally derived. Hence, weed seed mortality in the soil seedbank is likely to be influenced by the maternal environment and genetics. We hypothesized that seed accessions from contrasting maternal environments (seed lots) exhibit different rates of seed mortality and that the relative differences among seed lots remain consistent across burial environments. Velvetleaf and giant foxtail annual seed mortality rates were studied in field experiments in Hickory Corners, MI, and Wooster, OH, using seed lots collected from the same locations. Seeds enclosed within mesh bags and unenclosed seeds (''seeded cores'') exhibited similar levels of seedbank persistence ($r = 0.90$, $P < 0.001$) and seed mortality ($r = 0.65$, $P = 0.006$). Annual seed mortality rates ranged from 16 to 56% and 27 to 91% for seed lots of velvetleaf and giant foxtail, respectively. Relative differences among velvetleaf seed lots were consistent across burial environments in both years, whereas giant foxtail differences were consistent in only 1 of 2 yr. The relative ranks among velvetleaf seed lots varied between years, indicating that maternal environment may have influenced seed persistence more than seed-lot genetics. Within years, variation in seed mortality was predicted by changes in soil moisture in the burial environment ($R^2 = 0.47$, $P < 0.001$ for velvetleaf; $R^2 = 0.34$, $P = 0.007$ for giant foxtail). Accelerated seed mortality was associated with moist soils (soil water potential = −6 kPa for velvetleaf, −7 kPa for giant foxtail). These results suggest that agronomic practices affecting the maternal environment and moisture levels in the soil seedbank may promote weed seed mortality in the soil seedbank.
Nomenclature: Giant foxtail, *Setaria faberi* Herrm. SETFA; velvetleaf, *Abutilon theophrasti* Medik. ABUTH.
Key words: Hydrotime, seed burial methods, soil water potential, seed mortality, seed persistence.

Seed survival in the soil seedbank is vital to the continued existence of annual weed species (Cousens and Mortimer 1995), and therefore, successful management of summer annual weeds includes the depletion of the soil seedbank (Davis 2006). In conventional agricultural systems, weeds are artificially removed from the soil seedbank by stimulating germination by tillage and then mechanically or chemically destroying weed seedlings (Mohler 2001). An alternative for low external input agricultural systems is seedbank reduction through management of natural soil processes in a conservation biocontrol approach (Gallandt et al. 1999). Progress toward effective weed seedbank management methods will require a better understanding of weed seed biology and ecology in soil seedbanks.

The likelihood of seed mortality in the soil seedbank is influenced by the interaction between inductive factors in the environment and defensive mechanisms intrinsic to the seed (Fenner and Thompson 2005). Factors that cause seed mortality include soil microorganisms (Chee-Sanford et al. 2006; Kremer 1993) and the stimulation of germination in unfavorable conditions (Ellery and Chapman 2000). These causal factors of seed mortality are influenced by soil physical characteristics, such as soil water content (Mickelson and Grey 2006; Schafer and Kotanen 2003) and relative levels of soil carbon and nitrogen (Davis 2007). Therefore, rates of seed mortality vary in different burial environments (Skoglund and Verwijst 1989). A crucial defense against seed mortality is the seed coat. Seed coats often contain secondary metabolites, such as phenols and alkaloids, that inhibit microorganisms (Mohamed-Yasseen et al. 1994). Seed coats may also contain a continuous layer of densely packed, lignified cells that mechanically resist fungal penetration (Kremer et al. 1984). Furthermore, seed coats can impose seed dormancy through physical constraints on germination, thus preventing recruitment in conditions not conducive to seedling establishment (Bewley and Black 1994).

Seed coats are entirely derived from maternal tissues (Bewley and Black 1994) and are largely influenced by the maternal environment and genetics. For example, the altitude at which maternal plants were grown affected perennial goosefoot (*Chenopodium bonus-henricus* L.) seed coat thickness (Dorne 1981), maternal light environment influenced seed coat pigmentation of chayotillo (*Sicyos deppei* G. Don.) (Orozco-Segovia et al. 2000), and mouseear cress [*Arabidopsis thaliana* (L.) Heynh.] maternal genetics affected seed coat permeability to tetrazolium (Papi et al. 2002). The maternal influence on the seed's primary defense against mortality suggests that seed mortality rate varies among seed lots (seed accessions exposed to different maternal environments). Furthermore, if putative maternal effects are a primary determinant of seed mortality, relative differences among seed lots are expected to be maintained across burial environments. Although evidence for maternal effects on seed mortality is compelling, this idea has yet to be tested. Studies on the maternal influence on seed mortality are important so that potentially confounding population effects are excluded when developing ecologically based seedbank depletion strategies.

We investigated seed mortality of velvetleaf and giant foxtail within soil seedbanks 1 yr following dispersal. These species were chosen because they are common, economically important, summer annual weeds in corn (*Zea mays* L.) and soybean [*Glycine max* (L.) Merr.] fields in the Midwest United States (Bridges and Baumann 1992). Furthermore, the selected species exhibit contrasting seedbank dynamics, as velvetleaf populations are substantially more persistent than those of giant foxtail (Buhler and Hartzler 2001; Davis et al. 2005). We hypothesized that the annual seed mortality rate

DOI: 10.1614/WS-08-031.1
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varies among seed lots and that these differences are maintained across burial environments.

To approach the question of maternal and burial environment effect, we used two contrasting seedbank observation methods: buried bag and seeded core. The buried bag method buries a known number of viable seeds in mesh enclosures (hereafter referred to as *mesh bags*) for one or more years (Egley and Chandler 1978). Seeded cores consist of small volumes of soil spiked with a known number of seeds, nested within a larger core that is excavated at the end of the burial period (Teo-Sherrell et al. 1996). The buried bag method simplifies seed recovery compared with seeded cores, but a notable flaw in the buried bag method is that seedlings within mesh bags degrade within days to weeks, making seed mortality indistinguishable from germination following a prolonged burial period. Although the primary objective of this investigation was to determine maternal and burial environment effects on seed mortality, a secondary objective was to compare the buried bag and seeded core seedbank observation methods. We hypothesized that the buried bag method would give similar mortality results as seeded cores if the mesh bags were recovered during the germination period.

Materials and Methods

The experiment was designed as a factorial combination of two burial locations (Hickory Corners, MI [MI] and Wooster, OH [OH]), two seed lots (MI and OH), and two seedbank study methods (seeded core and buried bag). At each location, seed lots were arranged in a randomized complete-block design with four replications. The experiment was initiated in November of 2003 and November of 2004 and was terminated after 1 yr. Seed mortality was determined each year at both sites on March 18, June 15, and November 1.

The MI study site was an agricultural field at the Michigan State University Kellogg Biological Station (42°24′N, 85°24′W), and the OH study site was an agricultural field at the Ohio Agriculture Research and Development Center (40°47′N, 81°55′W). Before the study, corn and soybean were grown in rotation and under no-tillage at the MI site for 30 yr and at the OH site for 25 yr. The soil at the MI site was a Kalamazoo silt loam (Typic Hapludalf; 43% sand, 40% silt, 17% clay, 1.1% organic content), and the soil at the OH site was a Wooster loam (fine, mixed, Typic Fragiaqualf; 11% sand, 75% silt, and 14% clay, 2.9% organic content). Ambient seedbank densities of the study species were determined by collecting a 100-g soil sample paired with each experimental unit burial location, followed by mechanical elutriation for 30 min and drying at 35 C for 24 h (Wiles et al. 1996).

Seed lots consisted of seeds collected from spatially contiguous populations within fields at each study site. Seeds were hand-harvested by shaking mature seedheads over a bucket. No further seed cleaning took place. Seeds were stored for no longer than 1 mo in plastic, airtight containers at 5 C. Just before burial, initial viability for each lot was determined by tetrazolium assay with 1% (v/v) aqueous solution of 2,3,5-triphenyl-tetrazolium chloride (Peters 2000).

Mesh bags (10 cm by 10 cm), fabricated from 0.5-mm polyester mesh netting, contained 100 seeds, and were buried in holes (10 cm diameter, 5 cm deep) that were dug by removing soil plugs with a golf cup cutter.[1] Seeded cores were constructed by removing soil plugs (6 cm diameter, 5 cm deep) with cylindrical probes, placing 400 seeds at the bottom of each hole, and refilling holes with the original plugs. Soil plugs were handled carefully to prevent crumbling so that the bulk density of soil above the seeds was not altered. Once plugs were in place, the seams between the plugs and surrounding soil were pinched closed.

Beginning in early April and continuing until late July, seedlings were counted and removed from seeded cores every two weeks. To excavate seeded cores, a golf cup cutter[1] was used to pull a 10-cm-diam, 10-cm-deep soil plug that contained the original 6-cm-diam plug within a larger soil volume. Mesh bags were excavated with a trowel. Seeded cores and mesh bags were brought to the laboratory for seed recovery, which was accomplished by mechanical elutriation or hand-processing, respectively.

Seed retention was determined as the number of recovered seeds divided by the initial number of seeds. Recovered seeds were visually inspected and classified as intact, damaged, or germinated. Germinated seeds were those with radicles, including withered radicles. Viability of intact seeds was determined with tetrazolium assays of 30-seed samples. Seedbank persistence was determined as the number of viable seeds remaining divided by the number of viable seeds that were buried. Percentage of seed mortality (μ) was calculated using Equation 1:

$$\mu = \frac{(s_0 + a_0) - (s_1 + g)}{(s_0 + a_0)} \times 100 \qquad [1]$$

where s_0 is the number of viable seeds added at the start of the experiment, a_0 is the estimated number of ambient seeds present at the start of the experiment, s_1 is the number of viable seeds recovered at the end of the experiment, and g is either the total number of emerged seedlings from seeded cores or the total number of seeds that germinated in mesh bags. Mesh bags confound losses to seed mortality with losses to seedling recruitment after a prolonged burial period. Therefore, November 1 seed-mortality data for the buried bag method used germination counts from June 15. By this date, in a typical year, giant foxtail and velvetleaf emergence in the region is nearly complete (Hartzler et al. 1999).

Data Analysis. Seedbank study methods were compared by analyzing seed retention, seedbank persistence, and seed mortality data. The seed retention comparison used data collected on March 18, which is before the typical date of initial seedling emergence in the region (Hartzler et al. 1999). Therefore, potential seed loss from germination was minimized. Levene's test for homogeneity of variance (Neter et al. 1996) indicated unequal variance in seed retention between years; therefore, data for the 2 yr were analyzed separately. Retention data were analyzed with two-way ANOVA, using the GLM procedure of SAS.[2] Independent variables in the ANOVA included seedbank type, burial location, species, and the interactions between variables.

To compare seedbank persistence and seed mortality between mesh bags and seeded cores, we used data that was collected on November 1. Levene's test for homogeneity of variance indicated equal variance between years; therefore, data for the 2 yr were pooled. The degree to which mesh bags predicted seeded core mortality and persistence was determined via correlation analysis of seed lot means at each burial

location. Initially, correlation analysis was performed separately for giant foxtail and velvetleaf; however, the *F* test for comparing regressions (Zar 1999) indicated that least-squares regressions for individual species were estimates of the same population. Velvetleaf and giant foxtail data were then pooled. Statistical parameters to assess the agreement between seedbank types included Pearson's correlation coefficient and mean absolute errors (MAE) (Mayer and Butler 1993). MAE provides an indication of the typical difference between mesh bags and seeded cores in the same units as the data.

Maternal and burial environment effects on seed mortality were determined separately for mesh bags and seeded cores with data from November 1. Velvetleaf and giant foxtail data were analyzed independently, and within each species, years were separated because of heterogeneous variance as indicated by Levene's test. Within species and years, data met the requirements for ANOVA and were analyzed with the MIXED procedure of SAS. Fixed effects in the models were seed lot, burial location, and their interactions. Random effects were blocks nested within locations. The significance of fixed effects was determined using an *F* test. Variance component analysis (Edwards 1993) was performed to determine the relative influences of the following fixed effects on seed mortality: seed lot, burial location, the interaction between burial location and seed lot, and differences within seed lots at a burial location. A significance level of $\alpha = 0.05$ was used for all statistical tests.

In addition to annual contrast between burial locations, the influence of the burial environment on seed mortality was also examined on a subannual basis. Because soil moisture has previously been shown to influence seed mortality (Mickelson and Grey 2006; Schafer and Kotanen 2003), we studied the progression of seed mortality over the course of a year in response to changes in soil water potential. Daily soil water potentials (ψ_i) at the 5-cm depth were predicted from weather data with the Simultaneous Heat and Water (SHAW) 2.3 model (Flerchinger and Saxton 1989). Inputs for the SHAW model included latitude, longitude, elevation, slope, orientation, soil organic matter, % sand, % silt, % clay, and daily weather data (precipitation, air temperature, solar radiation, relative humidity, and wind speed). Weather data for SHAW were collected within 5 km of the study sites by weather stations programmed to record atmospheric conditions every 5 min.

For each site–year and for each species, mean percentage of seed mortality was determined for burial periods ending March 18, June 15, and November 1. Seed mortality proportion data were subjected to a logit transformation (Hosmer and Lemeshow 2000) and regressed on hydrotime. Hydrotime was calculated with daily soil water potential data as shown in Equation 2:

$$\theta_H = \sum_{i}^{n} M_i \qquad [2]$$

where M_i is 1 when $\psi_i > \psi_b$ (otherwise, M_i is 0), ψ_b is the base soil water potential for seed mortality and indicates the water potential below which seed mortality will not occur, and n represents the number of days in the study interval. Base soil water potentials for seed mortality have yet to be empirically determined. In this study, base soil water potentials were adjusted until the differences between predicted and actual mortality were minimized. We initiated the search for base soil water potentials at 0 kPa and proceeded in increments of 0.5 kPa to −10.0 kPa, at which point base water potentials were adjusted in increments of 5 kPa to −50.0 kPa. The *F* test for comparing linear models indicated that mesh bag and seeded core regressions of seed mortality on hydrotime were estimates of the same population, and Levene's test for homogeneity of variance indicated that variance was evenly distributed between mesh bags and seeded cores. Therefore, mesh bag and seeded core data were combined for hydrotime models.

Results and Discussion

Seedbank Study Methods. The buried bag method retained a higher percentage of seeds than seeded cores in 2004 ($P < 0.001$) and 2005 ($P < 0.001$); however, seed retention was not consistent across species and locations. In 2004, seeded cores retained fewer velvetleaf seeds than mesh bags (mean percentage of seed retention was 76 ± 3% for seeded cores, 97 ± 1% for mesh bags), but for giant foxtail, mean percentage of retention did not differ between mesh bags and seeded cores (91 ± 2%). In 2005, seeded cores at the MI location retained fewer seeds than mesh bags (60 ± 4% seed retention in seeded cores, 98 ± 0.5% seed retention in mesh bags), but at the OH location, mean percentage of seed retention was similar for both seedbank methods (94 ± 2%).

Seeds missing from seeded cores were probably not lost during recovery because in preliminary experiments where seeded cores were excavated immediately after installation, 95% of buried seeds were recovered (A. S. Davis, unpublished results). Furthermore, the recovered cores were larger than the original cores, and weed seeds are known to exhibit little inherent movement from their original burial position (Mohler et al. 2006). Teo-Sherrell et al. (1996) attributed seeds missing from seeded cores to fatal germination or seed decay rather than failure to find seeds. Further seed losses in seeded cores may have occurred by earthworms (Shumway and Koide 1994) or arthropods (Benvenuti 2007). Seed-retention differences between seeded cores and mesh bags suggest that, under particular conditions, mesh bags can inhibit seedbank demise and inflate predictions of seedbank persistence; however, in this study, seedbank persistence data for mesh bags corresponded well with seedbank persistence data for seeded cores (Figure 1).

To determine seed mortality, the buried bag method was modified by recovering mesh bags during the germination period, thus enabling estimations of seedling recruitment. The buried bag method tended to underestimate seed mortality compared with seeded cores, but in general, percent seed mortality values were similar between seeded cores and mesh bags (Figure 1). The slight discrepancy in percent seed mortality between mesh bags and seeded cores may have been because of differences in seed densities (14 seeds cm^{-2} in seeded cores, 1 seed cm^{-2} in mesh bags). Along these lines, Van Mourik et al. (2005) determined that, in densely packed mesh packets, increased seed-to-seed contact promoted fungal decay. An alternative explanation for the slight discrepancy between seedbank observation methods is that increased mortality in seeded cores represents seeds that germinated but failed to emerge. This suggests that fatal germination under natural conditions can be determined using the seeded core and buried bag methods in tandem.

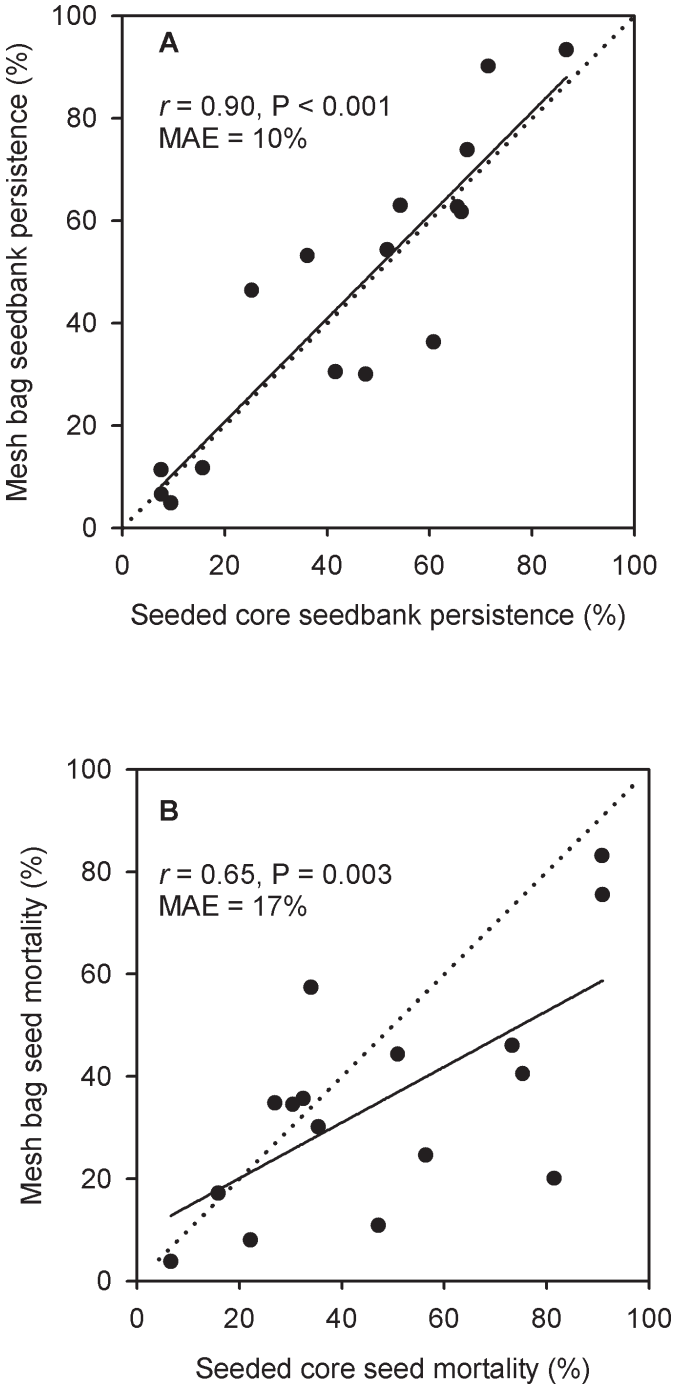

Figure 1. Correlation between mesh bags and seeded cores for (A) percentage of seedbank persistence and (B) percentage of seed mortality. Seedbank persistence and seed mortality were determined for velvetleaf and giant foxtail in two different years with seeds that were buried 5 cm for 1 yr. Symbols represent means of four replications of factorial combinations of seed lots from Ohio (OH) and Michigan (MI) and burial location (OH and MI). Dotted lines represent 1 : 1 correspondence, and solid lines represent linear regressions with mesh bags as the dependent variable, y, and seeded cores as the independent variable, x. The regression equation for seedbank persistence is $y = 1.01x + 0.51$, $P < 0.001$; and for seed mortality is $y = 0.55x + 9.22$, $P = 0.006$. MAE indicates mean absolute error.

Seed fate in the soil seedbank is crucial to population dynamics of annual weeds (Cousens and Mortimer 1995), yet methodological limitations have routinely prevented researchers from determining rates of seed mortality in large-scale field studies (for example, see Davis et al. 2005). By simplifying the seed recovery process and including an estimate of seedling recruitment, the modified buried bag method enables rates of seed mortality to be determined in multiple environments.

Table 1. Variance component analyses for seed mortality. Treatments consisted of factorial combinations of two seed lots from Ohio (OH) and Michigan (MI) and two burial locations (OH, MI). Mortality was determined with seeds buried 5 cm from November 9, 2003, to November 1, 2004, and from November 9, 2004, to November 1, 2005.

	Total variation in seed mortality[a]			
Source	ABUTH 2004	ABUTH 2005	SETFA 2004	SETFA 2005
	%			
Seed lot	53.5	46.3	39.6	11.7
Burial location	3.3	12.6	2.4	37.5
Lot by location interaction	10.6	7.4	2.5	3.8
Within seed lots at a burial location	32.5	33.8	55.5	47.0

[a] Abbreviations: ABUTH, velvetleaf; SETFA, giant foxtail.

Maternal and Burial Environment Effects on Annual Seed Mortality. Because seeded cores resemble natural soil seedbanks more closely than do mesh bags, we initially present the seeded core data for maternal and burial environment effects on seed mortality. Overall mean percentage of seedbank persistence was 59 ± 6% for velvetleaf and 31 ± 9% for giant foxtail. Seedbank persistence levels in this investigation were consistent with previous studies, which found that 38 to 57% of velvetleaf seeds and 21 to 49% of giant foxtail seeds remained after 1 yr of burial (Buhler and Hartzler 2001; Davis et al. 2005). In this study, seedbank persistence followed the natural inverse relationship ($r = -0.83$, $P < 0.001$) with seed mortality. Overall mean seed mortality was 25 ± 5% for velvetleaf and 46 ± 9% for giant foxtail.

Variation in velvetleaf seed mortality was primarily explained by differences among seed lots (Table 1). In 2004, the velvetleaf OH lot consistently exhibited greater seed mortality than the MI lot, and in 2005, the velvetleaf MI lot consistently exhibited greater mortality than the OH lot (Figure 2). These results support our hypothesis that seed mortality differences among seed lots are maintained in different burial environments and indicate that the inherent character of the seed population influenced velvetleaf seed mortality more than the burial environment. For giant foxtail seed mortality, the principal source of variation was within seed lots at a particular burial location (Table 1); however, seed lot and burial location effects were significant in 2004 and 2005, respectively (Figure 2). In 2004, the giant foxtail MI lot exhibited greater seed mortality than the OH lot at both burial locations. Interestingly, in 2004, the direction of the relationship between seed lots varied between species, which suggests that maternal effects that influence seed mortality are species specific.

All above results, except for the giant foxtail 2005 comparison, were corroborated by the buried bag method. When mesh bag data were introduced into the analysis, seed lot effects were again significant for velvetleaf in 2004 ($F_{1,21} = 11.3$, $P = 0.003$), velvetleaf in 2005 ($F_{1,21} = 54.2$, $P < 0.001$), and giant foxtail in 2004 ($F_{1,21} = 36.4$, $P < 0.001$). Although location effects on seed mortality for giant foxtail in 2005 were not significant when mesh bag data

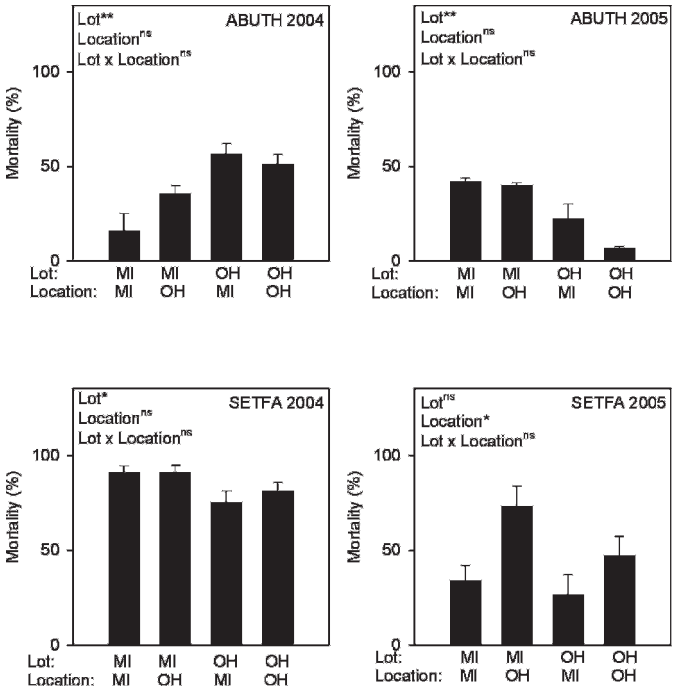

Figure 2. Percentage of seed mortality for factorial combinations of seed lots from Ohio (OH) and Michigan (MI) and burial location (OH and MI). Seeds were buried in seeded cores at 5 cm from November 9, 2003, to November 1, 2004, and from November 9, 2004, to November 1, 2005. Bars represent the means and standard errors of four replications. Insets contain the significance of *F* tests from two-way ANOVA. Significance: *, $P < 0.05$; **, $P < 0.01$. Abbreviations: ABUTH, velvetleaf; SETFA, giant foxtail.

were included ($F_{1,21} = 0.43$, $P = 0.43$), the mortality trend between locations remained the same (data not shown).

For giant foxtail in 2005, seed mortality was influenced by burial location because of low mortality levels at MI. Compared with all site-years of this study, MI in 2005 had exceptionally low precipitation levels (Table 2), which is a condition known to inhibit seed mortality in soil seedbanks (Mickelson and Grey 2006; Schafer and Kotanen 2003). Despite the extreme conditions at MI in 2005, mortality differences between velvetleaf seed lots were maintained. Therefore, maternal influences on seed fate were stronger in velvetleaf as compared with giant foxtail.

Velvetleaf seed lots were collected from the same locations in consecutive years. Neither collection location exhibited consistently high or low levels of seed mortality. This eliminated the possibility of high and low biotypes and suggested that the differences between velvetleaf seed lots in seed mortality were likely due to maternal environment effects. Maternal environment effects may have been mediated through the seed coat, which offer physical (Kremer et al. 1984), chemical (Kremer 1986), and physiological (Cardina and Sparrow 1997) resistance to seed mortality. Two previous studies indicated that velvetleaf seed coats are malleable to factors in the maternal environment. Nurse and DiTommaso (2005) found that velvetleaf seed coat weight decreased when maternal plants were grown with corn as compared with maternal plants grown with velvetleaf. Cardina and Sparrow (1997) noted that the level of coat-imposed seed dormancy for velvetleaf seed lots increased when maternal plants grew in warmer, drier conditions.

Environmental maternal effects can be adaptive if the factor that elicits the response provides information about the environment the progeny will encounter (Mousseau and Fox 1998). For example, the maternal light spectrum (in particular, red to far-red ratios) can influence offspring germination requirements and can indicate the competitive environment offspring will experience (Donohue and Schmitt 1998). In regard to seed mortality, this suggests that the prevalence of seed mortality agents in the maternal environment influences seed defenses against mortality; however, this speculation requires further research. Clarifying the factors in the maternal environment that influence seed mortality will not only indicate the adaptive significance of maternal effects but may also lead to novel management methods that reduce seed survivorship before seeds are dispersed from the maternal plants.

Subannual Burial Environment Effects on Seed Mortality. Gummerson (1986) proposed that rates of seed germination could be described by time spent above a threshold water potential, i.e., a hydrotime scale. We extended the hydrotime concept to describe variation in seed mortality observed over the course of a year. Hydrotime models explained more variance in velvetleaf and giant foxtail seed mortality than models based on thermal time, hydrothermal time, and day of year (Table 3). Therefore, among the parameters tested, soil moisture was the most influential condition on seed mortality and was suspected to have contributed to variation in seed mortality observed among burial locations (Figure 1).

Base soil water potentials for seed mortality have yet to be empirically determined. In this study, base soil water potentials were adjusted until the differences between predicted and actual mortality were minimized. The iterative process of adjusting base water potentials indicated that the highest rates of seed mortality for giant foxtail occurred in a continuous range from −30 kPa to −7 kPa, and the highest rates of seed mortality for velvetleaf occurred in two distinct moisture environments: −40 kPa and −6 kPa (Figure 3). Variation in threshold parameters may represent variation among individual seeds (Bradford 1996). Unlike giant foxtail seeds, which all freely imbibe (Dekker 2003), velvetleaf seed populations contain impermeable (hard) and permeable (soft) seeds (Lacroix and Staniforth 1964). Hardseededness in velvetleaf is due to the seed coat's palisade layer (Winter 1960), which is also critical in defense against fungal

Table 2. Precipitation totals at the Michigan (MI) study site (Hickory Corners, MI) and the Ohio (OH) study site (Wooster, OH) from April 1, 2003, to October 31, 2005.

	Precipitation				
Site	April 1, 2003, to October 31, 2003	November 1, 2003, to March 31, 2004	April 1, 2004, to October 31, 2004	November 1, 2004, to March 31, 2005	April 1, 2005, to October 31, 2005
	cm				
MI	54.9	51.3	52.9	42.8	40.9
OH	69.1	54.2	76.4	40.2	51.6

Table 3. Parameters describing the linear regressions of seed mortality for velvetleaf and giant foxtail as a function of hydrotime, thermal time, hydrothermal time, and day of year.[a]

Independent variable[b]	Species[c]	β_0 (± SE)	β_1 (± SE)	R^2	P value
Hydrotime[d]	ABUTH	−1.9 (0.18)	3.2×10^{-2} (8.0×10^{-3})	0.47	< 0.001
	SETFA	−1.7 (0.11)	7.0×10^{-2} (3.1×10^{-3})	0.34	0.007
Thermal time[e]	ABUTH	−1.5 (0.16)	2.0×10^{-4} (3.5×10^{-5})	0.23	0.03
	SETFA	−0.8 (0.46)	3.0×10^{-4} (7.0×10^{-4})	0.11	0.15
Hydrothermal time[f]	ABUTH	−1.5 (0.14)	2.3×10^{-3} (8.2×10^{-4})	0.30	0.01
	SETFA	−1.1 (0.42)	4.4×10^{-3} (1.6×10^{-3})	0.28	0.02
Day of year	ABUTH	−1.9 (0.26)	2.5×10^{-3} (1.0×10^{-4})	0.25	0.02
	SETFA	−1.4 (0.77)	4.6×10^{-3} (3.0×10^{-3})	0.12	0.14

[a] Seed mortality was measured at Hickory Corners, MI, and Wooster, OH, during 2004 and 2005.
[b] Regressions were in the form: *logit*(*proportion seed mortality*) = $\beta_0 + \beta_1 \times x$, where β_0 represents the y intercept, β_1 represents the slope of the regression line, and x represents the independent variable; $n = 20$.
[c] Abbreviations: ABUTH, velvetleaf; SETFA, giant foxtail.
[d] Base soil water potential is −7 kPa for giant foxtail and −6 kPa for velvetleaf.
[e] Base temperature is 1 C
[f] Calculated according to Gummerson (1986). Base parameters identical to those used for hydrotime and thermal time.

pathogens (Kremer et al. 1984). Hard seed coats are fractured by fluctuations in the moisture environment (Horowitz and Taylorson 1985; Lacroix and Staniforth 1964), and we propose that the extreme wet environment (−6 kPa) resulted in elevated internal osmotic pressure that weakened seed coats of hard seeds, thus making them susceptible to fungal decay. Seed coats of soft seeds did not require structural modification to be susceptible to fungal decay, and mortality occurred once there was enough water in the soil to move fungal pathogens to velvetleaf seeds (−40 kPa). High rates of seed mortality may also have been due to hypoxic conditions associated with high soil matrix potentials (Thompson 2000). Although the mechanisms of seed mortality are not clear from this study, our results suggest that seed death is a rapid phenomenon, representing a catastrophic failure rather than a gradual erosion of viability. We base this assumption on the fact that soil conditions associated with the highest rates of mortality occurred for only 20 to 39 d yr^{-1}.

Managing the soil environment to promote seed mortality has been proposed as a method for weed seedbank depletion (Davis 2007; Mickelson and Grey 2006); however, high soil water potentials are not practical during the growing season because hypoxic conditions damage crop roots (Lambers et al. 1998). A useful approach to accelerate seed mortality may be to manage the soil environment so that drainage is delayed when crops are absent. Based on the results of this study, soils would need to be saturated for approximately 37 d yr^{-1} to kill 95% of giant foxtail seeds and 79 d yr^{-1} to kill 95% of velvetleaf seeds. It is unclear whether saturated conditions should occur as a continuous period or separate events.

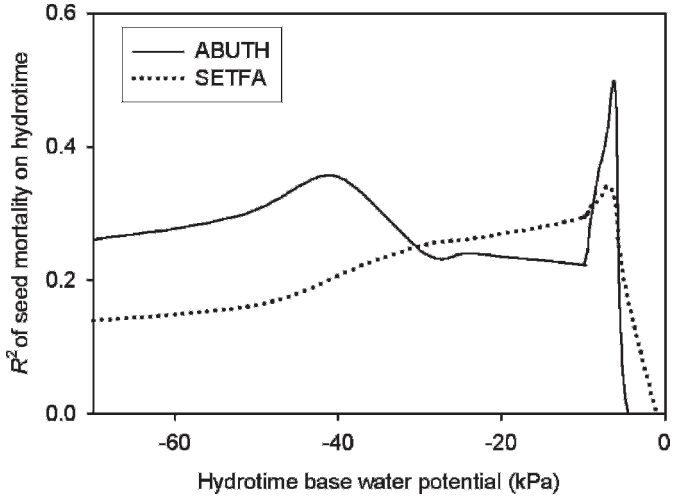

Figure 3. R^2 values for linear regressions of hydrotime against seed mortality across a range of base water potentials. Abbreviations: ABUTH, velvetleaf; SETFA, giant foxtail.

The vitality of velvetleaf seeds, coupled with velvetleaf's strong maternal influence on seed mortality, indicate that to promote velvetleaf seed mortality through conservation biocontrol, management methods will need to consider the environment in which seeds were produced in addition to the burial moisture environment. Subsequent research should attempt to identify the factors that induce maternal effects on seed mortality and explore the mechanisms of seed mortality under high soil moisture levels. Once these causal factors of seed mortality have been clarified, ecologically based strategies for seed bank depletion will need to be devised and validated in many crop environments.

Sources of Materials

[1] Lever extraction hole cutter, Coursigns, Inc., Lake Forest, IL 60045.
[2] SAS Institute, Inc., SAS Campus Drive, Cary, NC 27513-2414.

Acknowledgments

This work was supported in part by the USDA Sustainable Agriculture Special Grants program and the USDA Agricultural Research Service. Mention of trade names or commercial products in this article is solely for the purpose of providing scientific information and does not imply recommendation or endorsement by the U.S. Department of Agriculture.

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Received February 14, 2008, and approved August 12, 2008.